Chapter 7
Seed Dispersal by Cattle: Natural History and Applications to Neotropical Forest Restoration and Agroforestry

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7.1 Introduction

Agricultural expansion in Latin America is intimately associated with tropical deforestation and biodiversity loss (e.g. Angelsen and Kaimowitz 2001). Although agricultural activities are frequently abandoned (Aide and Grau 2004), their effects on forest regeneration processes may be much more persistent (e.g. Ferguson et al. 2003). On land subjected to prolonged and/or heavy use, potential for forest recovery is limited by the dearth of tree seedlings, resprouts and seed banks (Uhl et al. 1990). At such sites, seed dispersal from off-site is the principal colonization route for woody plants. However, distance to seed sources, lack of seed disperser activity, seed predation, herbivory, poor soils, high light intensity, frequent fires and competition with herbaceous ground cover impede forest regeneration from seed rain (Holl 1998b, 1999, Meli 2003).

Among the most common of these barriers is the lack of animals capable of transporting seed between wooded and open areas (Holl 1999, Guariguata and Ostertag 2002, Meli 2003). Animals disperse as many as 66% of tree species in Neotropical forests, principally by swallowing and defecating their seed (Howe and Smallwood 1982, Wunderle Jr. 1997). The major dispersers are birds and bats, although primates, rodents and other mammals may play a complementary part. Many wild seed dispersers, particularly forest birds, do not cross open areas (Wunderle Jr. 1997). Frugivorous birds that do enter open areas generally limit their activities to patches of woody vegetation within the agricultural landscape, and their movements depend upon plant phenology, particularly fruiting period. The result is a scanty seed rain that is heterogeneous in both space and time (da Silva et al. 1996, Wunderle Jr. 1997).

Restoration ecologists have proposed techniques to overcome or bypass this barrier to tropical forest regeneration. Such techniques include the manual collection and planting of tree seeds and/or seedlings and the artificial establishment of structural diversity to attract dispersers to open areas (McClanahan and Wolfe 1993, Holl 1998a, Holl and Kappelle 1999, Parrotta and Knowles 1999). While these efforts have met with some success, they can be costly to implement at large scale (Lamb et al. 2005).

Another option for reestablishing tree cover over large areas arises from the observations of Janzen and Martin (1982), who argued that numerous Central American trees are adapted for dispersal by large herbivores. When much of the Pleistocene megafauna went extinct around 10,000 years ago, they maintain, numerous tree species were left without efficient dispersers. Since colonial times, seeds of many such trees have been dispersed by introduced livestock, particularly cattle and horses.

Under the right circumstances, cattle, a salient feature of many Neotropical landscapes, are indeed important seed dispersal agents. Where management permits, cattle cross easily between secondary forests, younger fallows, and pastures (Hernández and Benavides 1995), and may also be rotated through fields to graze on crop residues (Jiménez Ferrer et al. 2003). They eat the fruit of a wide variety of trees and shrubs (Moreno Casasola 1996), and their digestive processes are mild enough to leave many seeds intact (Razanamandranto et al. 2004, Pascacio Damián 2006). Furthermore, light grazing can diminish the competitive effect of grasses on woody colonizers (Posada et al. 2000) another important barrier to tree establishment (Holl et al. 2000, Posada et al. 2000).

Although many instances of seed dispersal by cattle (hereafter referred to as "bovinochory") are known, systematic studies of the relationship are lacking. We review ecological and agronomic literature to typify bovinochorous trees and shrubs and describe the methods used to study the phenomenon. We describe fruits, seeds and habitat of the species involved, quantify reports of bovinochory by plant family and summarize the authors' conclusions with regard to the impact of bovinochory. Next, taking the ecologically diverse state of Chiapas, Mexico as a case study, we analyze the management potential of bovinochory as a tool for reestablishing woody plant cover under both active cattle production and ecological restoration scenarios. We present preliminary interview and sampling data identifying woody bovinochores in Chiapas, then combine information from interviews and literature review to describe the distribution, physiological requirements, uses and aptitude as successional nuclei of these species. Finally, we propose a research agenda to support full realization of bovinochory's management potential.

7.2 Methods

7.2.1 Literature Review

Between September, 2004 and June, 2006, we consulted databases including Science Citation Index expanded (ISI web of science, 1951–2005), Google Scholar and the Livestock, Environment and Development Digital Library (lead.virtualcentre.org). Search terms included combinations of "seed dispersal," or "germination," and "livestock," "cattle," or "bovine," in both English and Spanish. We also searched for articles citing Janzen and Martin (1982). We carried out additional searches to develop descriptions of the characteristics of each species relevant to their dispersal, habitats, uses and potential function as successional nuclei.

7.2.2 Chiapas Field Studies

During 2005 and 2006 we conducted interviews on 60 ranches to identify bovinochorous, woody species in both the wet and dry lowlands of Chiapas. During both the wet and dry seasons, we surveyed dung pats on the same ranches for germinating seedlings. We also collected dung and sieved a portion for seeds while spreading the rest over soil-filled trays in the greenhouse to facilitate germination. This work is ongoing and the preliminary results are reported here as a case study of the management potential of bovinochory. Details of the methodology will be provided elsewhere (Miceli Méndez In prep.).

7.3 Results

7.3.1 Studies Identified and Their Methodologies

Our searches identified 38 articles that mention 24 bovinochorous, woody species (cited here by the scientific names utilized by the Missouri Botanical on mobot.mobot.org; Table 7.1). We classify these according to the methodology they employed to study bovinochory as experimental, descriptive and/or modeling. The experimental studies include germination trials of seed banks in pasture soil and dung (Gutiérrez and Armesto 1981, Janzen et al. 1985, Somarriba 1986, Peinetti et al. 1993, Campos and Ojeda 1997, Brown and Archer 1999, Doucette et al. 2001, Villagra et al. 2002, Kneuper et al. 2003, Razanamandranto et al. 2004) as well as trials of pregermination treatments (McCully 1951, Argaw et al. 1999, Rubio-Delgado et al. 2002). Other experimental trials compared the effectiveness of simulated bovine digestion with those of other scarification treatments (Janzen et al. 1985, Somarriba 1986). Studies described as observational/descriptive mainly documented foraging behaviour, presence of viable seed in dung and the distribution of seedlings. Their data come from both field observations and interviews. The modeling studies simulated the population dynamics of bovinochorous species under differing management scenarios (Radford et al. 2001, Tews et al. 2004).

7.3.2 Characteristics of Bovinochores

Sixteen of the 24 bovinochorous species identified belong to the Fabaceae family, two species are Rosaceae, and 6 other families, Boraginaceae, Caprifoliaceae, Myrtaceae, Rutaceae, Sterculiaceae, and Tiliaceae, are represented by a single species each (Fig. 7.1). Two of these families are in the same order (Malvales) but no other relationships are apparent at this taxonomic level. Of the Fabaceae, 14 species are in the Mimosoideae subfamily and two are Ceaesalpinoideae.

Table 7.1 Cattle-dispersed woody plants reported in the literature and further findings regarding bovinochory

Species	Type of study	Findings	Country	Study
Acacia caven (Mol.) Molina *Mimosoideae* Fabaceae	E	• Germination of seeds extracted from dung was 5 times that of seed extracted directly from pods.	Chile	(Gutiérrez and Armesto 1981)
Acacia dudgeoni Craib ex Hall *Mimosoideae* ***Acacia seyal*** Del. Mimosoideae ***Burkea africana*** *Hook. f.* *Caesalpinioideae* ***Prosopis africana*** (Guill., Perrott. & Rich.) Taub. *Mimosoideae* Fabaceae	E	• Due to the larger diameter of their digestive systems, cattle affect viability and germination of these four species less than sheep do. • The moist, acid environment of dung may accelerate germination. • Large herbivores may plan a major role in long-distance seed dispersal.	Burkina Faso	(Razanamandranto et al. 2004)
Acacia farnesiana (L.) Willd. *Mimosoideae* Fabaceae	D	• Colonization of pastures and other disturbed areas by these species results from bovinochory (a). • Cattle can disperse large amounts of viable seed (b)	USA México	a) (Parrotta 1992) b) (Pascacio Damián 2006)

Acacia nilotica L. Willd. ex Del. *Mimosoideae* Fabaceae	D M	• This is an invasive plant in Australian rangelands. • Its invasive power is a product of prolific seed output and efficient dispersal by cattle (80% of seeds defecated intact) • Only 1% of seed in sheep dung is intact. • Models predict patchy invasion related to microclimate and water sources for livestock.	Australia	(Radford et al. 2001)
Acacia pennatula Schldl. & Cham. Benth. *Mimosoideae* Fabaceae	D (a–c) E(d)	• The range of this species has increased due to human activity (d). • Cattle disperse its seeds (a–e). • Seedlings grow directly from cattle dung (b, c) • Germination is greatest in the shade (d). • The size distribution varies in response to canopy cover and disturbance intensity (d). • This species seems to facilitate colonization by other woody plants (d).	Mexico (a, d, e) Nicaragua (b) Costa Rica (c)	a) (Greenberg et al. 1997) b) (Nieto et al. 2001) c) (Ibrahim and Camargo 2001) d) (Rubio-Delgado 2001) e) (Pascacio Damián 2006)

(continued)

Table 7.1 (continued)

Species	Type of study	Findings	Country	Study
Acacia tortilis (Forsk.) *Mimosoideae* Fabaceae ***Dichrostachys cinerea*** *Mimosoideae* Fabaceae	D E	• A majority of seeds of both species, consumed in their pods by cattle, were still viable upon defecation (while seeds of *Acacia senegal*, *A. seyal*, and *Balanites aegyptiaca* were not). • Seed of all 5 species collected from the soil, under tree canopies, and from barns germinated in the laboratory. • The abundance and breadth of seed distribution of *A. tortilis* and *D. cinerea* is a result of bovinochory. • Seeds of both species were most numerous in barns.	Ethiopia	(Argaw et al. 1999)
Citrus limetta RissoRutaceae ***Cordia curassavica*** (Jacq.) Roem. & Schult. Boraginaceae	D	• Farmers report bovinochory. • Seedlings sprout from cattle dung.	Nicaragua	(BGF pers. obs.)
Dichrostachys cinerea (L.) Wight & Arn.Fabaceae (see also *Acacia tortilis*)	D (a, c) E (b)	• This treelet, introduced to Cuba from Madagascar, is considered an invasive pest although it has multiple domestic and industrial uses (a, c). • Cattle disperse this species (c,b) and are the principal cause of its invasion of Cuban pastures (a).	Cuba (c), Etiopía (a–b)	a) (Mabberley 1997) b) (Argaw et al. 1999) c) (Méndez Santos and Ramos Jalil 2004)

Enterolobium cyclocarpum (Jacq.) Griseb. Mimosoideae Fabaceae	D (a, c) E (b)	• Cattle and horses consume the seeds, favoring their germination from dung and soil (a, c). • *In vitro* simulations of bovine and equine digestion found that seeds defecated within a day of ingestion survive at rates of 11 and 9% respectively. Longer retention reduces viability (b).	Costa Rica (a–c)	a) (Janzen and Martin 1982) b) (Janzen et al. 1985) c) (Ibrahim and Camargo 2001)
Grewia flava Tiliaceae	M	• This is an invasive species in rangelands. • Cattle distribute the seed into open grassland. • Simulations predict that bovinochory promotes invasion.	South Africa	(Tews et al. 2004)
Guazuma ulmifolia Lam. Sterculiaceae	D (a–c)	• Cattle consume and disperse the seeds, favoring establishment on degraded lands (a, b). • Bovinochory favors germination (a). • This species was likely dispersed by extinct Pleistocene megafauna (a). • This species favors colonization by other woody plants (c).	Guatemala (b) Costa Rica (b, c)	a) (Janzen 1982b) b) (Ferguson 2001) c) (Ibrahim and Camargo 2001)

(continued)

Table 7.1 (continued)

Species	Type of study	Findings	Country	Study
Pithecellobium saman Benth *Mimosoideae* Fabaceae	D (a, b)	• The species is bovinochorous (a, b). • This is a multipurpose species suitable for silvopastoral systems (a).	Australia (a) Costa Rica (b)	a) (Durr 2001) b) (Ibrahim and Camargo 2001)
Prosopis caldenia Burkart *Mimosoideae* Fabaceae	D, E	• The fruit is valuable forage. • The gradual increase in this species' range is due to bovinochory. • The species can become a pest as a result of bovinochory. • Excreted seed exhibited lower viability and higher germinability than uningested seed.	Argentina	(Peinetti et al. 1993)
Proposis flexuosa DC *Mimosoideae* Fabaceae	E	• Bovinochory favors germination more than dispersal by other wild and domestic animals (a, b). • However, seeds obtained directly from the tree exhibit greater viability than those defecated by cattle (a). • Both cattle and Patagonian maras (*Dolichotis patagonum*) separate seeds from their endocarp, favoring germination (a, b).	Argentina	a) (Campos and Ojeda 1997) b) (Villagra et al. 2002)

Prosopis juliflora (Sw.) DC (synonym of ***Prosopis glandulosa*** Torr. var. Glandulosa) *Mimosoideae* Fabaceae	E (a, b) D (b, c)	• Cattle defecate viable seed (b, c). • However, seed consumed by sheep and goats are less viable (b). • Cattle may accelerate invasion of rangelands by this species (a). • Invasion is homogeneous and independent of ground cover (a).	USA (a, b) Ethiopia (c)	a) (Brown and Archer 1999) b) (Kneuper et al. 2003) c) (Shiferaw et al. 2004)
Psidium guajava L. Myrtaceae	D (a, b, d, e) E (c)	• Cattle disperse the seeds, favoring seedling establishment (d,e). • During peak fruiting, cattle may consume 49,500 seeds/day (a,b). • The number of seeds dispersed diminishes with increasing fruit size (a,b). • Simulated bovine digestion did not affect seed germination (c). • This species can become a pest in tropical rangelands as a result of bovinochory (d).	Costa Rica (a–d) Colombia (e)	a) (Somarriba 1985a) b) (Somarriba 1985b) c) (Somarriba 1986) d) (Somarriba 1995) e) (Esquivel Sheik and Calle Díaz 2002)

(continued)

Table 7.1 (continued)

Species	Type of study	Findings	Country	Study
Rosa bracteata Wendl. Rosaceae	D, E (a, b)	• Cattle defecate viable seed of this species (a, b). • Approximately 80% of seeds consumed were recovered between the second and third days following ingestion (a). • Eight % of defecated seeds were physically damaged (a). • Bovinochory favors germination (a). • Seeds that remain in dung maintain their viability (a). • The species is an invasive exotic in SE USA (a, b).	USA	a) (McCully 1951) b) (Douce et al.)
Rosa woodsii Lindl Rosaceae ***Symphoricarpos albus*** (L.) BlakeCaprifoliaceae	E	• Viability following excretion by cattle was 77.4 and 69.3% respectively. • Cattle could be managed to disseminate these species. • *R. woodsii* invades rangelands.	Canada	(Doucette et al. 2001)
Senna atomaria (L.) H.S.Irwin & BarnebyFabaceae		• Cattle can disperse large amounts of viable seed.		(Pascacio Damián 2006)

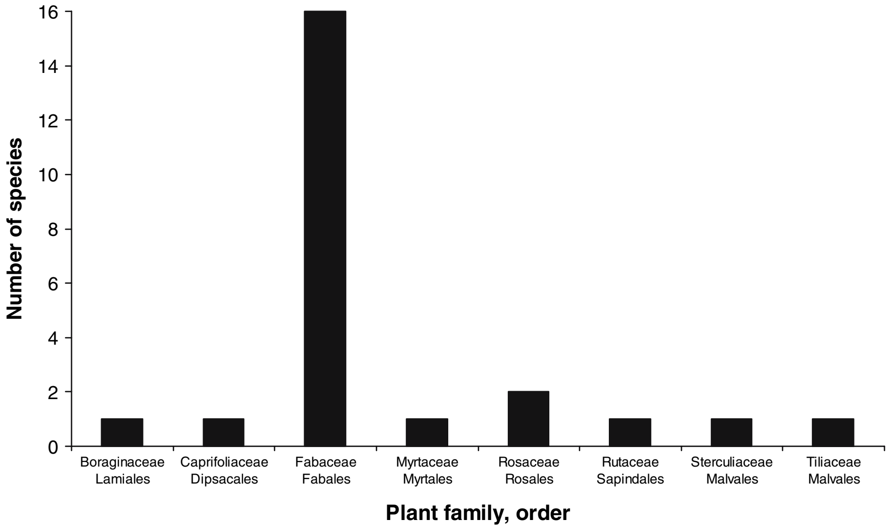

Fig. 7.1 Cattle-dispersed woody plants reported in the literature, by botanical family and order

The fruits of these species are variously dry and indehiscent (n=16), dry and dehiscent (n=1) or fleshy (n=7); drab (n=13), yellow (n=4), red-orange (n=4) or white (n=1); and may be fragrant or without odor. The mean fruit length for species for which data could be found is 10.3 ± 6.6 (standard deviation) cm. The typical bovinochorous fruit is a legume with dry, elongated, indehiscent, brown-black pods.

Seeds of bovinochorous are also highly variable. Their mean length is 7.0 ± 4.2 mm, with a range of 2–23 mm. Seed weight averages 83 ± 154 mg across species, ranging from 4 to 700 mg. Appendix 1 provides detailed descriptions of bovinochorous seeds and fruits.

7.3.3 Where does Bovinochory Occur?

The studies we identify report bovinochory of trees and shrubs in North, Central and South America, the Caribbean, Africa and Australia. They describe bovinochory in tropical and temperate savannas and, less frequently, in areas where the native vegetation is deciduous or semi-deciduous tropical dry forest, tropical rain forest or pine-oak forest (Table 7.1).

7.3.4 Effects of Bovinochory on Seed Fate

Cattle digestive processes often have minimal effect on seed viability and germination (Peinetti et al. 1993, Razanamandranto et al. 2004). However scarification in the bovine digestive tract may soften the seed coat, both diminishing the proportion of viable seed and accelerating germination of surviving seed (Janzen et al. 1985, Doucette et al. 2001). For several species (*Acacia dudgeoni, Acacia seyal, Rosa woodsii, Symphoricarpos albus, Burkea africana, Prosopis africana*), viability varies inversely with duration of retention in the digestive tract (Doucette et al. 2001, Razanamandranto et al. 2004). Small, smooth seeds tend to pass more rapidly and suffer less damage (Razanamandranto et al. 2004). Cattle digestion augments germination rate more than other physical and chemical treatments for some species, including *Enterolobium cyclocarpum, Psidium guajava, Rosa bracteata, Rosa woodsii*, and *Symphoricarpos albus* (McCully 1951, Janzen et al. 1985, Somarriba 1986, Doucette et al. 2001).

The molar mill may also play a role in scarification, as in the case of the *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. In a series of scarification trials, this palm germinated only after being chewed and spit out by cattle (Orantes García 1999).

Cattle dung can be a propitious microsite for germination and establishment of some plants. Dung provides both an acid environment in which further scarification takes place, and abundant nutrients for seedling growth (Somarriba 1986, Razanamandranto et al. 2004). Species exhibiting increased establishment in dung microsites include *Acacia dudgeoni, Acacia seyal, Burkea africana, Prosopis africana, Prosopis flexuosa* (Villagra et al. 2002, Razanamandranto et al. 2004, Loth et al. 2005).

7.3.5 Bovinochory in Chiapas

The state of Chiapas, Mexico is an appealing context in which to explore the ecology and management of bovinochory for several reasons: (1) it affords a broad range of topographic and climatic conditions, resulting in a correspondingly broad variety of ecosystems (González-Espinosa et al. 2005); (2) these ecosystems host extraordinary biological diversity, including 9 of the 24 bovinochorous species reported in Table 7.1; (3) cattle ranching is of economic and social importance throughout the state, and is practiced under a variety of management scenarios. In this section, we report preliminary results of extensive surveys designed to identify further bovinochorous species in lowland Chiapas.

The ranchers surveyed identified a total of 17 woody species that germinate from cattle dung, including representatives of the Anacardiaceae, Burseraceae, Bignoniaceae, Cactaceae, Fabaceae, Malpighiaceae, Moraceae, Myrtaceae, Rutaceae, Sapotaceae, Sterculiaceae, Ulmaceae and Tiliaceae. Of these, we have thus far confirmed the presence of viable seed of 12 tree species and one shrub species in cattle dung. Eight of the trees have been previously reported as bovinochorous.

While our surveys focused on lowland Chiapas, our literature and database searches found that the 13 confirmed bovinochorous species are distributed across a broad range of ecosystems (Miranda 1998, Pennington and Sarukhán 1998). Most are not frost-resistant, but at least three species reach altitudes of 2,000 m or more.

All 13 grow in the dry lowlands and five are also present in the humid tropics. This suite of species also grows across a spectrum of soil types, from rich soils of volcanic origin to calcareous soils, to highly-weathered, acidic soils.

7.4 Discussion

Notably, most of the studies we identify in our literature review treat one or a few bovinochorous species, often as invasive plants that present a challenge to rangeland management (Brown and Acher 1989). Some of these cases present dramatic demonstrations of the influence of bovinochory on the composition and structure of plant communities. However, few studies (e.g. Argaw et al. 1999) attempt to identify the suite of bovinochorous plants in a given system and we found no systematic studies designed to identify bovinochorous species in the Neotropics. Nonetheless, our review and findings from Chiapas corroborate Janzen and Martin's (1982) generalizations regarding the importance of livestock as dispersal agents for neotropical trees and shrubs. We are able to draw some useful conclusions regarding characteristics of bovinochorous species, when and how bovinochory occurs, and how the phenomenon might be exploited for both enhancement of tropical rangelands and for catalyzing ecological restoration.

7.4.1 The Ecology of Bovinochory

As Janzen and Martin (1982) predicted, bovinochorous fruits are highly variable in size, color, morphology, odor, nutrient composition, seed size, etc., defying definition of a consistent bovinochorous dispersal syndrome (Howe 1985). Indeed, as Bruun and Poschlod (2006) note, cattle and other ungulates may be important vectors for many species without obvious dispersal adaptations. One generalization that does seem to hold true is that the seeds are hard and smooth, protected within a hard, smooth nut, or else very small (Janzen and Martin 1982).

While legumes with indehiscent pods are disproportionately favored by cattle, bovinochory manifests itself across numerous plant families (Fig. 7.1). Janzen and Martin (1982) mention species from 14 plant families in Pacific lowland, deciduous forest of Costa Rica that are dispersed by livestock and/or may have been dispersed by extinct megafauna. Eleven of these families (Anacardiaceae, Arecaceae, Bignoniaceae, Bromeliaceae, Fabaceae, Malpighiaceae, Moraceae, Myrtaceae, Sapotaceae, Sterculiaceae, Tiliaceae) along with three additional families (Burseraceae, Cactaceae, Rutaceae) are represented among the species we have thus far identified in Chiapas as bovinochorous.

Both the literature and our preliminary data suggest that bovinochory is more prevalent in dry forest areas than in the humid tropics. This observation is consistent with the hypothesis that bovinochory is a characteristic inherited from coevolution with large, extinct herbivores that maintained, savanna-like vegetation (Janzen and Martin 1982). Such plants must have been able to survive in the relatively dry microclimate of these open areas and could be expected to be most abundant in today's dry forests.

Bovinochory has been reasonably well documented in the range management context (e.g. McCully 1951, Brown and Acher 1989, Cox et al. 1993, Auman et al. 1998, Doucette et al. 2001, Bruun and Fritzboger 2002, Edwards and Younger 2006). However, its influence upon successional patterns in abandoned neotropical pastures seems to have been largely disregarded by ecologists since Janzen and Martin (1982), perhaps because of the more obvious association between cattle and deforestation (Hecht 1993).

Intriguingly, we and the ranchers we have interviewed have observed latency in seeds of cattle-dispersed taxa, including *Acacia*, spp. and *Guazuma ulmifolia*, species that are often important early-successional colonizers (e.g. Ferguson et al. 2003). Thus these species may germinate not from post-abandonment seed rain, but from a seed bank that accumulates in pastures during years of use. Draft animals and livestock grazing on crop stubble may also contribute to seed banks and successional patterns in croplands.

Furthermore, the structural diversity and resources provided by bovinochores that establish in active pasture doubtless also play a role in post-abandonment succession. In open vegetation, structural diversity is vital to maintaining seed dispersal by wild animals, and isolated trees offer key microsites for establishment of other woody species (Guevara et al. 1986, Vieira et al. 1994, da Silva et al. 1996, Ferguson 2001). In the Central Valleys of Chiapas, bovinochorous trees including *Enterolobium cyclocarpum*, *Pithecelobium dulce*, *Guazuma ulmifolia*, *Acacia pennatula,* and *Acacia farnesiana* are salient features of the landscape. These trees can offer important habitat for birds (e.g. Greenberg et al. 1997), contributing to successional dynamics.

7.4.2 Management Potential of Bovinochory in the Neotropics

Strategies that contribute simultaneously to rural livelihoods and biological conservation are urgently needed throughout the Neotropics (Sánchez et al. 2000, Angelsen and Kaimowitz 2001). Our findings with respect to the diversity of Neotropical bovinochorous trees and shrubs, the range of ecosystems in which they grow and the apparent importance of bovinochory in structuring vegetation in grazing land in the dry tropics all highlight the potential for management of this relationship. Establishment of trees via bovinochory holds particular promise for both silvopastoral systems and ecological restoration. This strategy could be used to plant trees at low cost by exploiting relationships and resources already familiar to rural people.

7.4.2.1 Silvopastoral Systems

Silvopastoral systems rely on trees, particularly multiple-use trees to improve the productivity of grazing land (Sánchez 1998). Our searches found multiple uses for all of the bovinochorous trees and shrubs we report from Chiapas. In addition to forage, these plants offer wood for diverse applications, extracts for tanning, shade for coffee or cattle, medicine, perfume, soil retention, wind breaks and live fences among other products and services (Miranda 1998).

Availability of quality forage in the dry season is a major determinant of the productivity of Neotropical rangelands (Botero and Russo 1998). Most bovinochorous species fruit during the dry season when grasses are less abundant and cattle seek alternative forage. Their fruits and seeds generally possess high concentrations of lipids, proteins and soluble carbohydrates that both attract and nourish livestock (Chargoy Zamora 1988, Razanamandranto et al. 2004). We have identified several ranchers in the Central Valleys who use trees dispersed by their cattle as key dry season forage. One of these ranchers relies on bovinochory to establish *Acacia pennatula*, thinning the trees as necessary to maintain a favorable balance between trees and grass. Two more ranchers use cattle-dispersed *Guazuma ulmifolia,* and one of them spread *G. ulmifolia* seed across his ranch intentionally by feeding its fruits to his cows. These ranchers report that within 3 months of germination, *G. ulmifolia* can withstand frequent browsing. In addition to high quality forage, *G. ulmifolia* provides firewood, wood, and medicine (CATIE 1991, Miranda 1998, Pennington and Sarukhán 1998). Other bovinochorous species that may represent considerable forage resources in Chiapas include *Acacia farnesiana, Enterolobium cyclocarpum*, *Manilkara achras, Nopalea dejecta*, *Parmentiera aculeata*, *Pithecellobium* spp., *Prosopis juliflora*, *Psidium guajava, Senna atomaria y Senna spectabilis*.

7.4.2.2 Restoration

Where ecological restoration is the primary management objective, bovinochory may catalyze successional processes by increasing woody plant seed rain in open areas and diversifying microsites for establishment. Bovinochorous colonizers help re-establish the vegetation structure and food resources that attract wild seed vectors, which in turn will diversify the seed rain. Seeds deposited by wild dispersers will find improved microsites for germination and recruitment under bovinochorous plants (e.g. Ferguson 2001). Thus two of the most frequent barriers to forest regeneration in tropical pastures, lack of seed rain and of safe sites for establishment of woody plants (Holl et al. 2000), may be overcome by bovinochory.

Several bovinochores hold considerable potential as successional nuclei. All colonize open areas and most tolerate poor soils (CATIE 1991, Miranda 1998, Pennington and Sarukhán 1998). Many such early colonizers improve soil conditions or microclimate or attract seed-dispersing wildlife (Vieira et al. 1994, Meli 2003). Some, such as *A. pennatula*, *G. ulmifolia* and *P. dulce* are of particular importance for wildlife conservation (Greenberg et al. 1997, Leon-Cortes et al. 2004, B.G.F. pers ob.). However some bovinochorous species, including *Acacia* spp., *D. cinerea*, *Prosopis* sp. and *P. guajava* form dense thickets that could impede colonization by other species or restrict cattle movement and the productivity of rangelands (Peinetti et al. 1993, Somarriba 1995, Méndez Santos and Ramos Jalil 2004).

7.4.3 Research Priorities

Despite the success of some of the ranchers we interviewed at managing bovinochory, broad and efficient exploitation of this phenomenon will require deeper understanding of its ecology and natural history. Here we outline some pertinent areas of research.

The range of plant species susceptible to bovinochory has yet to be studied in most places. Interviews with ranchers, observations of germination in dung pats, controlled germination of seed from dung and simple experiments involving the addition of seeds or fruits to livestock diets may all quickly yield this kind of information.

Differences among livestock species and even breeds with respect to their capacity for seed dispersal should also be explored. We have focused on cattle as the most ubiquitous livestock in neotropical landscapes. However horses are also effective seed dispersers and they use different habitat and graze different species than do cattle (Cosyns et al. 2005). Sheep, while less likely than cattle to excrete whole seeds (Razanamandranto et al. 2004), are locally important in tropical highlands (Jiménez Ferrer et al. 2003), while tropical sheep are increasingly grazed in the lowlands (Nuncio-Ochoa et al. 2001).

The distribution and characteristics of various microsites arising from bovinochory influence seed and seedling fate. Patterns of dung deposition correspond to herbivores' habitat preferences and can be influenced by management (Wiegand et al. 1999, Cosyns et al. 2005). Dung pats can create short-lived gaps in dominant vegetation (Cosyns et al. 2006, Kohler et al. 2006), offer an acid environment that scarifies seed, and provide nutrients that favor seedling establishment (Razanamandranto et al. 2004). Dung beetles may act as secondary dispersers, diversifying the range of microsites encountered by bovinochores, but may also bury seed well below the soil surface where establishment is unlikely (Díaz Valdiviezo 2005). Microsite conditions arising from bovinochory and secondary dispersal are likely to favor some species in some environments, while filtering out others.

Changes in management of grazing lands bovinochory can alter the significance of bovinochory over a range of spatial scales. In northern Europe, for example, a reduction in the number of free-ranging livestock, increased fencing of pastures and less common long-distance seasonal movement of livestock have all contributed to a decline in seed dispersal in modern times (Bruun and Fritzboger 2002). Recent changes in Mexico's land reform law permitting division and sale of *ejido* land may similarly alter patterns bovinochory in that country. At the same time, enforcement of bans on burning seems to be favoring increased tree cover, particularly of bovinochores, in some ranching-dominated landscapes of the Central Valleys of Chiapas.

Grazing pressure likely interacts with bovinochory to determine germination and establishment rates. Intriguingly, because cattle generally prefer herbaceous forage, woody plant establishment can be greater at low livestock densities than in the absence of grazing where grasses are unchecked (Posada et al. 2000, Tobler et al. 2003). Thus cattle may simultaneously increase seed rain and lessen competition faced by establishing seedlings. However the form of the relationship between grazing pressure and woody plant establishment is little known as is the effect of timing of grazing in relation to germination. Further complicating this relationship, well-timed grazing may reduce fuel loads and thus the frequency and severity of fire during early succession (Fonseca and Beita In press).

For purposes of both restoration and silvopastoral systems, we need a better understanding of the interactions of bovinochorous shrubs and trees with other species. Which bovinochores permit or even favor grass growth beneath their crowns, and which grasses are most compatible with them (Hernández-Daumas 2000)? Conversely, which create shade levels or other microsite conditions that favor establishment of more woody plants (Vieira et al. 1994)? Which create habitat for wildlife species of interest (e.g. Greenberg et al. 1997), particularly for wild seed dispersers (Vieira et al. 1994)? Which species, under what conditions, are likely to form dense stands, and which maintain wider spacing that permits continued grazing and/or establishment of other species (Peinetti et al. 1993)? Does early dominance by bovinochores cause a "founder effect" that influences successional trajectory over the long term (Drake 1991)?

7.5 Conclusions

Cattle ranching is justifiably viewed as a major agent of neotropical deforestation (e.g. Hecht 1993). However under some conditions, seed dispersal and grazing by cattle can overcome major barriers to reestablishment of woody cover in open areas, catalyzing successional processes. Exploitation of this relationship holds promise as a cheap, efficient tool for both silvopastoral systems and ecological restoration. Further research will help realize the full potential of this strategy across a range of tropical ecosystems.

Acknowledgment We thank Mario Alberto López Miceli, Ivonne Anahí López Miceli, María Guadalupe Pascacio Damián, María Lesvia Dominguez Morales, Henry Castañeda Ocaña, Miguel Martínez Icó and Juan López Méndez for valuable support in the field, laboratory, greenhouse and herbarium. We are also grateful to Lorena Soto Pinto and René Pinto Ruíz for comments on an early draft. This research was supported by the Fondo sectorial CONACyT-SEMARNAP through the project "Uso sustentable de los Recursos Naturales en la Frontera sur de México", SEMARNAT-2002-C01-1109.

Appendix

Appendix 1 Characteristics of fruits and seeds of woody plants cited in the literature as cattle-dispersed

	Fruit			Seed				
Species and growth form	Type (Moreno 1984)	Color	Size Length × width × thick-ness (cm)	Shape	Mass (mg)	Size Length × width × thickness (mm)	Fruiting season	Source
Acacia caven (Mol.) Molina Shrub/Tree	Dry indehiscent, thick, oblong	Brown to black, shiny.	5 × 2	Compressed, smooth, ellispsoid	115.1	7.5	Dec.–April	(CIAT/FAO, Sánchez de Lorenzo-Cáceres, Piaggio 2003)
Acacia dudgeoni Craib ex Hall Tree/Shrub	Dry indehiscent, oblong, flattened, glabrous	Brown	5.5 × 2	NA	8.54	8.2 × 8.2 × 1.8	Dec.	(CIAT/FAO, Razanamandranto et al. 2004).
Acacia farnesiana (L.) Willd. Tree/Shrub	Dry indehiscent, sessile or on short stem, cylindrical-fusiform	Brown to black	5.5 × 1.3	Elliptical, reniform	83	6.6 × 4.7	Jan.–May	(PROCYMAF, Sánchez de Lorenzo-Cáceres, Standley et al. 1946–1975, Parrotta 1992, Vázquez-Yanes et al. 1999, Cordero and Boshier 2003, Pascacio Damián 2006)
Acacia nilotica L. Willd. ex Del. Tree	Dry indehiscent, woody	Brown to black	12.5 × 1.8	Ellipsoid, smooth, compressed	95.2	6.5 × 4.8	Mar.–June	(NewCROP, Sánchez de Lorenzo-Cáceres, Winrock International, Radford et al. 2001)

Acacia pennatula Schldl. & Cham. Benth. Tree	Dry indehiscent, woody, sessile, turgid	Brown	12.5 × 2.1 × 0.8	Globose, elliptical, hard, smooth	60.60	7 × 4.3 × 3.5	Nov.–Jan.	(Standley et al. 1946–1975, Missouri Botanical Garden, Martínez 1992, Miranda 1998, Rubio-Delgado 2001, Pascacio Damián 2006)
Acacia tortilis (Forsk.). Tree/Shrub	Dry indehiscent, glabrous or pubescent	Brown	10 × 0.7	NA	33.33	5.5	Oct.–Dec.	(FAO, Sánchez de Lorenzo-Cáceres, Winrock International, Duke 1983, Argaw et al. 1999, Loth et al. 2005)
Acacia seyal Del. Tree	Dry dehiscente, falcada, glabra	Brown	13.5 (length) × 0.7(thick-ness)	Elliptical, compressed, wrinkled, funiculate, elongate	3.83	6.6 × 4.2 × 3.1	April	(Sánchez de Lorenzo-Cáceres, Razanamandranto et al. 2004)
Burkea africana Hook. F.Tree	Dry indehiscent, pubescent, elliptical	NA	6 × 2.5	NA	10	8.1 × 6.1 × 2.5	Jan.	(CIAT/FAO, Razanamandranto et al. 2004)
Brosimum alicastrum *Sw*Tree	Globose with fleshy pericarp	Yellowish green, orangish red	2.3	Spherical with flattened tips, papery testa	1750	11.8 × 15 × 15	Mar.–May	(Pennington and Sarukhán 1998) Orantes et al. 2007
Citrus limetta Risso. Tree	Fleshy, exocarp thin and smooth	Pale yellow	5.8 × 6.1	Ovoid	170	11.6 × 5.8 × 4.4	Apr.–Jun.	(Miranda 1998, Miceli Méndez In prep.)
Cordia curassavica Shrub	Fleshy	Red	3.7 × 4.2 × 5.9	Ovoid	NA	3.7 × 4.2 × 5.9	Apr.–Nov.	(Missouri Botanical Garden)

(continued)

Appendix 1 (continued)

	Fruit			Seed				
Species and growth form	Type (Moreno 1984)	Color	Size Length × width × thickness (cm)	Shape	Mass(mg)	Size Length × width × thickness (mm)	Fruiting season	Source
Dichrostachys cinerea (L.) Wight & Arn. Shrub/Tree	Dry indehiscent, glabrous, oblong	Brown	6 × 1.1	Biconvex, obovate, elliptical, subcircular	29.41	4 × 3	Aug.	(FAO Feed Resources Group, ISSG)
Enterolobium cyclocarpum (Jacq.) Griseb. Tree	Dry indehiscent, woody, curved	Brown	5.5 × 7.1 × 1.2	Ovoid, flattened and hard	700	23 × 15	Mar.–May	(Standley et al. 1946–1975, Janzen 1982a, Janzen et al. 1985, Miranda 1998, Pennington and Sarukhán 1998)
Grewia flava Shrub	Fleshy	NA	NA	NA	NA	NA	End of rainy season	(Tews et al. 2004)
Guazuma ulmifolia Lam. Tree	Dry indehiscent, woody, ellipsoid	Black with small protuberances, hard	2.2 × 1.8	Spheroid	6.1	1.8 (diameter)	Sep.– Apr.	(Missouri Botanical Garden, Janzen 1982b, Miranda 1998, Pennington and Sarukhán 1998, Villatoro 1998, Vázquez-Yanes et al. 1999)

Parmentiera aculeata (Kunth) Seemann/Tree	Fleshy, elongate with longitudinal furrows	Yellowish green	15×6.5	Thin, hard	NA	NA	Jan.–Dec.	(PROCYMAF, Miranda 1998, Pennington and Sarukhán 1998)
Pithecellobium saman Benth. Tree	Dry indehiscent, linear, compressed	Brown	17.5×1.2	Oblong	175.43	6.5	Feb.–May	(Standley et al. 1946–1975) (Sánchez de Lorenzo-Cáceres, Miranda 1998, Zamora et al. 2001)
Prosopis africana (Guill., Perrott. & Rich.) Taub. Tree	Dry indehiscent, cylindrical	Dark red	15×3	NA	15.71	$8.7 \times 5.8 \times 4.0$	Feb.–Mar.	(CIAT/FAO, Razanamandranto et al. 2004)
Prosopis caldenia Burkart. Tree	Dry indehiscent	Dark yellow with violet spots	15	Ovoid	24.09	$6.1 \times 3.7 \times 2.2$	Dec.–Mar.	(CIAT/FAO, Peinetti et al. 1993, Cosiansi et al. 2003)
Proposis flexuosa DC.Tree	Dry indehiscent, soft exocarp, tic mesocarp	Straw-colored with violet to black splotches	16.5×1.0	Ovoid	32.35	$6.8 \times 4.5 \times 2.3$	Dec.–Jan.	(CIAT/FAO, Campos and Ojeda 1997, Villagra et al. 2002, Cosiansi et al. 2003)
Prosopis juliflora (Sw.) DC Tree	Dry indehiscent, elongate, compressed, glabrous	Yellow to violet	18.5×1.3	Round to oval	36.36	$7.5 \times 5.3 \times 3$	Jan.–May	(CIAT/FAO, Martínez 1992, Moreno Casasola 1996, Miranda 1998, Shiferaw et al. 2004)

(continued)

Appendix 1 (continued)

	Fruit			Seed				
Species and growth form	Type (Moreno 1984)	Color	Size Length × width × thick-ness (cm)	Shape	Mass(mg)	Size Length × width × thickness (mm)	Fruiting season	Source
Psidium guajava L.Tree	Fleshy, globose to ovoid	Yellowish cream to pink, fragrant, sweet-sour	8 (diameter)	Round to triangular	NA	4	Jul.–Feb.	(Somarriba 1985b, 1986, Moreno Casasola 1996, Pennington and Sarukhán 1998)
Rosa bracteata Wendl. Shrub	Fleshy, globose	Orange to red	NA	NA	NA	NA	NA	(Douce, Moorhead and Bargeron)
Rosa woodsii Lindl Shrub	Fleshy, globose to elipsoid	Red	0.9 (diameter)	Oval, hard	13.6	4.5 × 2.5	Aug.	(Johnson and Hoagland, Doucette et al. 2001)
Senna atomaria (L.) H. S. Irwin & BarnebyTree	Dry indehiscent, linear-cylindrical	Dark brown	28.5 × 1	Hard, smooth	36.36	5.2 × 2.8	Feb.–Jun.	(Palma and Román 2000, Cordero and Boshier 2003, Pascacio Damián 2006)
Symphoricarpus albus (L.) Blake Shrub	Fleshy, globose	White	NA	NA	4.6	3 × 1.2	NA	(USDA, Doucette et al. 2001)

References

Aide, T. M., and Grau, H. R. 2004. Globalization, migration, and Latin American ecosystems. Science 305:1915–1916.
Angelsen, A., and Kaimowitz, D. Eds. 2001. Agricultural Technologies and Tropical Deforestation. Wallingford, UK: CABI.
Argaw, M., Teketay, D., and Olsson, M. 1999. Soil seed flora, germination and regeneration pattern of woody species in an Acacia woodland of the Rift Valley in Ethiopia. Journal of Arid Environments 43:411–435.
Auman, B. S., Call, C. A., and Wiedmeier, R. D. 1998. Crested wheatgrass establishment in livestock dung deposited on degraded rangeland vegetation types in the Intermountain West, USA. Arid Soil Research and Rehabilitation 12:317–333.
Botero, R., and Russo, R. O. 1998. Utilización de árboles y arbustos fijadoras de nitrógeno en sistemas sotenibles de producción animal en suelos ácidos tropicales. In Agroforestería para la producción animal en Latinoamérica (electronic conference), eds. M. Rosales M., and M. D. Sánchez, pp. 171–192. Rome: FAO. http://lead-es.virtualcentre.org/es/ele/conferencia1/Agrofor1.htm.
Brown, J. R., and Acher, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (Prosopis glandulosa var. glandulosa) on sites differing in herbaceous biomass and grazing history. Oecologia 80:19–26.
Brown, J. R., and Archer, S. 1999. Shrub invasion of grassland: Recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80:2385–2396.
Bruun, H. H., and Fritzboger, B. 2002. The past impact of livestock husbandry on dispersal of plant seeds in the landscape of Denmark. Ambio 31:425–431.
Bruun, H. H., and Poschlod, P. 2006. Why are small seeds dispersed through animal guts: large numbers or seed size per se? Oikos 113:402–411.
Campos, C. M., and Ojeda, R. A. 1997. Dispersal and germination of Prosopis flexuosa (Fabaceae) seeds by desert mammals in Argentina. Journal of Arid Environments 35:707–714.
CATIE. 1991. Guácimo (Guazuma ulmifolia): Especie de árbol de uso múltiple en América Central. Turrialba, Costa Rica: Centro Agronómico Tropical de Investigación y Enseñanza.
Chargoy Zamora, C. I. 1988. Digestión Ruminal (Ecología y Evolución). Chapingo, Mexico: Universidad Autónoma Chapingo.
CIAT/FAO. Grassland species profiles.http://www.fao.org/ag/AGP/AGPC/doc/GBASE/. Accessed on February 2006.
Cordero, J., and Boshier, D. H. 2003. Árboles de Centroamérica: un Manual para Extensionistas. Oxford, UK, Costa Rica: Oxford Forestry Institute (OFI), Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).
Cosiansi, J. F., Hayipanteli, S., Alvarez, V., Da Riva, D., and Milanesi, E. 2003. Efecto de las características del fruto de Prosopis caldenia "caldén" en la calidad y eficacia de trilla de las unidades con púas de flujo tangencial helicoidal. Agriscientia 20:45–52.
Cosyns, E., Bossuyt, B., Hoffmann, M., Vervaet, H., and Lens, L. 2006. Seedling establishment after endozoochory in disturbed and undisturbed grasslands. Basic And Applied Ecology 7:360–369.
Cosyns, E., Claerbout, S., Lamoot, I., and Hoffmann, M. 2005. Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. Plant Ecology 178:149–162.
Cox, J. R., Dealbaavila, A., Rice, R. W., and Cox, J. N. 1993. Biological and physical factors influencing Acacia constricta and Prosopis velutina establishment in the Sonoran Desert. Journal of Range Management 46:43–48.
da Silva, J. M. C., Uhl, C., and Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conservation Biology 10:491–503.
Díaz Valdiviezo, J. L. 2005. Efecto de los Escarabajos Coprófagos (Coleoptera: Scarabaeidae) en el Destino de Semillas Presentes en Estiércol Vacuno. Licenciatura thesis. Universidad de Ciencias y Artes de Chiapas, Tuxtla Gutiérrez, Mexico.

Douce, G. K., Moorhead, D. J., and Bargeron, C. T. Invasive.org. www.invasive.org. Accessed on February 2006.

Doucette, K. M., Wittenberg, K. M., and McCaughey, W. P. 2001. Seed recovery and germination of reseeded species fed to cattle. Journal of Range Management 54:575–581.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. The American Naturalist 137:1–26.

Duke, J. A. 1983. Acacia tortilis (Forsk.). Hayne Handbook of Energy Crops.

Durr, P. A. 2001. The biology, ecology and agroforestry potential of the raintree, Samanea saman (Jacq.) Merr. Agroforestry Systems 51:223–237.

Edwards, A. R., and Younger, A. 2006. The dispersal of traditionally managed hay meadow plants via farmyard manure application. Seed Science Research 16:137–147.

Esquivel Sheik, M. J., and Calle Díaz, Z. 2002. Árboles aislados en potreros como catalizadores de la sucesión en la Cordillera Occidental Colombiana. Agroforestería en las Américas. CATIE 9(33–34):43–47.

FAO. Red Latinoamericana de Cooperación Técnica en Sistemas Agroforestales. http://www.fao.org/Regional/LAmerica/redes/sisag/arboles/.

FAO Feed Resources Group. Animal Feed Resources Information System. http://www.fao.org/AG/AGA/AGAP/FRG/AFRIS/default1.htm. Accessed on February 2006.

Ferguson, B. G. 2001. Seed dispersal by livestock accelerates succession in a degraded neotropical field. (Guatemala). Ecological Restoration 19:115–116.

Ferguson, B. G., Vandermeer, J., Morales, H., and Griffith, D. M. 2003. Post-agricultural succession in the Maya lowlands. Conservation Biology 17:818–828.

Fonseca, G. W., and Beita, A. M. In press. El bosque seco tropical en Costa Rica: caracterización ecológica y acciones para la restauración. In Restauración de Bosques en América Latina, ed. M. González-Espinosa, J. M. Rey-Benayas, and N. Ramírez-Marcial, México DF: Ediciones Mundi-Prensa y Fundación Internacional para la Restauración de Ecosistemas.

González-Espinosa, M., Ramírez-Marcial, N., Méndez-Dewar, G., Galindo-Jaimes, L., and Golicher, D. 2005. Riqueza de especies de árboles en Chiapas: variación espacial y dimensiones ambientales. In Diversidad Biológica en Chiapas, eds. M. González-Espinosa, N. Ramírez-Marcial, and L. Ruiz-Montoya, pp. 81–125. México, DF: Plaza y Valdés.

Greenberg, R., Bichier, P., and Sterling, J. 1997. Acacia, cattle and migratory birds in Southeastern México. Biological Conservation 80:235–247.

Guariguata, M. R., and Ostertag, R. 2002. Sucesión secundaria. In Ecología y Conservación de Bosques Neotropicales, ed. M. R. Guariguata and G. H. Kattan, pp. 591–623. Cartago, Costa Rica: Libro Universitario Regional.

Guevara, S., Purata, S. E., and Van der Maarel, E. 1986. The role of remnant forest trees in tropical secondary succession. Vegetatio 66:77–84.

Gutiérrez, J. R., and Armesto, J. J. 1981. El rol del ganado en la dispersión de las semillas de Acacia caven (Leguminosae). Ciencia e Investigación Agraria 8:3–8.

Hecht, S. 1993. The logic of livestock and deforestation in Amazonia. Bioscience 43:687–695.

Hernández-Daumas, S. 2000. Carbon and Nitrogen Balance in a Tree-Grass Inter-Cropping System in the Humid Tropics of Mexico. Doctoral thesis. University of Edinburgh, Edinburgh.

Hernández, S., and Benavides, J. 1995. Potencial forrajero de especies leñosas de los bosques secundarios de El Petén, Guatemala. Agroforestería en las Américas 2:15–22.

Holl, K. D. 1998a. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restoration Ecology 6:253–261.

Holl, K. D. 1998b. Effects of above- and below-ground competition of shrubs and grass on Calophyllum brasiliense (Camb.) seedling growth in abandoned tropical pasture. Forest Ecology and Management 109:187–195.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31:229–242.

Holl, K. D., and Kappelle, M. 1999. Tropical forest recovery and restoration. Trends in Ecology and Evolution 14:378–379.

Holl, K. D., Loik, M. E., Lin, E. H. V., and Samuels, I. A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology 8:339–349.

Howe, H. F., and Smallwood, J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Howe, H. F. 1985. Gomphothere fruits: a Critique. American Naturalist 125:853–865.

Ibrahim, M., and Camargo, J. C. 2001. ¿Cómo aumentar la regeneración de árboles maderables en potreros? Agroforestería en las Américas. CATIE 8(32):35–41.

ICRAF. AgroForestryTree Database. http://www.worldagroforestrycentre.org/SEA/Products/AFDbases/AF/index.asp. Accessed on February 2006.

ISSG. Global Invasive Species Database. http://www.issg.org/database/welcome/. Accessed on February 2006.

Janzen, D. H. 1982a. Horse response to Enterolobium cyclocarpum (Leguminosae) fruit crop size in a Costa Rican deciduous forest pasture. Brenesia 19/20:209–219.

Janzen, D. H. 1982b. Natural history of guacimo fruits (Sterculiaceae, Guazuma umifolia) with respect to consumption by large mammals. American Journal of Botany 69:1240–1250.

Janzen, D. H., Demment, M. W., and Robertson, J. B. 1985. How fast and why do germinating guanacaste seeds (Enterolobium cyclocarpum) die inside cows and horses. Biotropica 17:322–325.

Janzen, D. H., and Martin, P. S. 1982. Neotropical anachronisms - the fruits the gomphotheres ate. Science 215:19–27.

Jiménez Ferrer, G., Soto Pinto, L., and Marquez Rosano, C. 2003. Ganadería en zona indígenas del sur de México: un reto para el desarrollo. In Sistemas Pecuarias Diversificados para el Alivio de la Pobreza Rural en América Latina (conferencia electrónica) FAO/CATIE. http://lead-es.virtualcentre.org/es/ele/conferencia4/programa.htm.

Johnson, F. L., and Hoagland, B. W. Catalog of the Woody Plants of Okalahoma. http://www.biosurvey.ou.edu/shrub/cover.htm. Accessed on February 2006.

Kneuper, C. L., Scott, C. B., and Pinchak, W. E. 2003. Consumption and dispersion of mesquite seeds by ruminants. Journal of Range Management 56:255–259.

Kohler, F., Gillet, F., Gobat, J. M., and Buttler, A. 2006. Effect of cattle activities on gap colonization in mountain pastures. Folia Geobotanica 41:289–304.

Lamb, D., Erskine, P. D., and Parrotta, J. A. 2005. Restoration of degraded tropical forest landscapes. Science 310:1628–1632.

Leon-Cortes, J., Perez-Espinoza, F., Marin, L., and Molina-Martinez, A. 2004. Complex habitat requirements and conservation needs of the only extant Baroniinae swallowtail butterfly. Animal Conservation 7:241–250.

Loth, P. E., de Boer, W. F., Heitkönig, I. M. A., and Prins, H. H. T. 2005. Germination strategy of the East African savanna tree Acacia tortilis. Journal of Tropical Ecology 21: 9509–517.

Mabberley, D. J. 1997. The Plant Book, 2nd edition. Cambridge: Reino Unido.

Martínez, C. B. 1992. Colecta de leguminosas silvestres con potencial forrajero. Licenciatura thesis. Universidad Autónoma de Chiapas, Villaflores, Chiapas, México.

McClanahan, T. R., and Wolfe, R. W. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology 7:279–288.

McCully, W. G. 1951. Recovery and viability of Macartney rose seeds fed to cattle. Journal of Range Management 4:101–106.

Meli, P. 2003. Restauración ecológica de bosques tropicales. Veinte años de investigación académica. Interciencia 28:581–589.

Méndez Santos, I. E., and A. Ramos Jalil. 2004. El marabú: ¿plaga o recurso natural? http://www.cubasolar.cu/biblioteca/energia/Energia27/HTML/articulo03.htm.

Miceli Méndez, C. L. In prep. Efecto del Ganado Bovino y Ungulados Silvestres en la Dispersión de Semillas de Especies Leñosas en Agropaisajes. Doctoral thesis. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas.

Miranda, F. 1998. La Vegetación de Chiapas, 3rd edition. Tuxtla Gutiérrez, Mexico: Gobierno del Estado de Chiapas, CONECULTA.

Missouri Botanical Garden. W3TROPICOS. http://mobot.mobot.org/W3T/Search/vast.html. Accessed on February 2006.

Moreno Casasola, P. 1996. Vida y Obra de Granos y Semillas. México, D F: Fondo de Cultura Económica.

Moreno, N. P. 1984. Glosario Botánico. Xalapa, Veracruz, Mexico: Compañía Editorial Contienental, Instituto Nacional de Invesigación Sobre Recursos Naturales.

NewCROP. New Crops Resource Online Program. http://www.hort.purdue.edu/newcrop/. Accessed on February 2006.

Nieto, H., Somarriba, E., and M. Gómez. 2001. Contribución de Acacia pennatula (carbón) a la productividad agroforestal sostenible de la Reserva Natural Miraflor- Moropotente. Estelí, Nicaragua. Agroforestería en las Américas. CATIE 8(30):21–23.

Nuncio-Ochoa, G., Nahed-Toral, J., Díaz-Hernández, B., Escobedo-Amezcua, F., and Salvatierra-Izaba, B. 2001. Caracterización de los sistemas de producción ovina en el Estado de Tabasco. Agrociencia 35:469–477.

Orantes García, C. 1999. Importancia de la testa y el endocarpo en la latencia de Acrocomia mexicana Karwinsky ex martius (coyol). Licenciatura thesis. Universidad de Ciencias y Artes del Estado de Chiapas, Tuxtla Gutiérrez, Chiapas.

Orantes G., C., Méndez, C. L. M., Ramírez, E. R. G., Méndez, A. M. V., and Moreno, R. A. M. 2007. Generación de Metodologías para la Propagación Sexual en Vivero de Tres Especies Tropicales con Potencial de Uso Forestal, Forrajero y Alimenticio en Chiapas. UNICACH-Fundación Produce, Tuxtla Gutierrez, Mexico.

Palma, J. M., and Román, L. 2000. Frutos de especies arbøreas leguminosas y no leguminosas para la alimentación de rumiantes. In II Conferencia Electrønica sobre Agroforestería para la Producciøn Animal., eds. M. D. Sánchez and M. Rosales Méndez, Rome. FAO-CIPAV. http://www.virtualcentre.org/es/ele/conferencia2/vbconfe15.htm.

Parrotta, J. A. 1992. Acacia farnesiana (L.) Willd. Aroma, huisache, Leguminosae (Mimosoideae). Report SO-ITF-SM-49. New Orleans, USA: US Dept. of Agriculture Forest Service, Southern Forest Experiment Station.

Parrotta, J. A., and Knowles, O. H. 1999. Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecology 7:103–116.

Pascacio Damián, M. G. 2006. Influencia del paso por el tracto digestivo y defecación por ganado bovino sobre el destino de semillas de tres fabaceas de bosque tropical subcaducifolia, en el Ejido La Florida Municipio de Cintalapa, Chiapas. Licenciatura thesis. Universidad de Ciencias y Artes de Chiapas, Tuxtla Gutiérrez, Chiapas.

Peinetti, R., Pereyra, M., Kin, A., and Sosa, A. 1993. Effects of cattle ingestion on viability and germination rate of calden (Prosopis-caldenia) seeds. Journal of Range Management 46:483–486.

Pennington, T. D., and J. Sarukhán. 1998. Arboles tropicales de México, 2nd edition. México, DF: Universidad Nacional Autónoma de México/Fonda de Cultura Económica.

Piaggio, M. 2003. Plantas Nativas de Uruguay. http://micol.fcien.edu.uy/flora/uy_flora.htm.

Posada, J. M., Aide, T. M., and Cavelier, J. 2000. Cattle and weedy shrubs as restoration tools of tropical montane rainforest. Restoration Ecology 8:370–379.

PROCYMAF. Especies con Usos No Maderables en Bosques de Encino, Pino y Pino-Encino. http://www.semarnat.gob.mx/pfnm/indices.html. Accessed on February 2006.

Radford, I. J., Nicholas, D. M., Brown, J. R., and Kriticos, D. J. 2001. Paddock-scale patterns of seed production and dispersal in the invasive shrub Acacia nilotica (Mimosaceae) in northern Australian rangelands. Austral Ecology 26:338–348.

Razanamandranto, S., Tigabu, M., Neya, S., and Oden, P. 2004. Effects of gut treatment on recovery and germinability of bovine and ovine ingested seeds of four woody species from the Sudanian savanna in West Africa. Flora 199:389–397.

Rubio-Delgado, L. 2001. Distribución de Acacia pennatula (Schldl.& Cham.) Benth. en bosques perturbados del norte de Chiapas, México. MS thesis. ECOSUR, San Cristóbal de las Casas, Mexico.

Rubio-Delgado, L., Ramírez-Marcial, N., and Castellanos-Albores, J. 2002. Distribución y regeneración de Acacia pennatula (Schltdl. & Cham.) Benth. en bosques perturbados del norte de Chiapas, México. Brenesia 57–58:67–84.

Sánchez de Lorenzo-Cáceres, J. M. Árboles Ornamentales. http://www.arbolesornamentales.com/.

Sánchez, M. D. 1998. Sistemas agroforestales para intensificar de manera sostenible la producción animal en Latinoamérica tropical. In Agroforestería para la Producción Animal en Latinoamérica, ed. M. Rosales, E. Murgueitio, H. Osorio, M. D. Sánchez, and A. Speedy, pp. 1–12, Roma: FAO-CIPAV. http://lead.virtualcentre.org/es/ele/conferencia1/sanchez1.htm. Accessed on February 2006.

Sánchez, M. D., Rosales, M., and Murgueitio, E. 2000. Agroforestería pecuaria en América Latina. In Segunda Conferencia sobre Agroforestería para la Produccíon Animal en America Latina FAO-CIPAV.

Shiferaw, H., Teketay, D., Nemomissa, S., and Assefa, F. 2004. Some biological characteristics that foster the invasion of Prosopis juliflora (Sw.) DC at Middle Awash Rift Valley Area, northeastern Ethiopia. Journal of Arid Environments 58:135–154.

Somarriba, E. 1985a. Árboles de guayaba (Psidium guajava L.) en pastizales. I. Producción de fruta y potencial de dispersión de semillas. Turrialba 35(3):289–295.

Somarriba, E. 1985b. Arboles de guayaba (Psidium guajava L.) en pastizales. II. Consumo de fruta y dispersión de semillas. Turrialba 35:329–332.

Somarriba, E. 1986. Effects of livestock on seed germination of guava (Psidium guajava L.). Agroforestry Systems 4:233–238.

Somarriba, E. 1995. Guayaba en potreros: establecimiento de cercas vivas y recuperación de pasturas degradadas. Agroforestería en las Américas. CATIE. Año 2 No. 6:27–29.

Standley, P. C., Steyermark, J. A., Williams, L. O., and Gibson, D. N. 1946–1975. Flora of Guatemala (Fieldiana).

Tews, J., Schurr, F., and Jeltsch, F. 2004. Seed dispersal by cattle may cause shrub encroachment of Grewia lava on southern Kalahari rangelands. Applied Vegetation Science 7:89–102.

Tobler, M. W., Cochard, R., and Edwards, P. J. 2003. The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. Journal of Applied Ecology 40:430–444.

Uhl, C., Nepstad, D., Buschbacher, R., Clark, K., Kauffman, B., and Subler, S. 1990. Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines for designing sustainable land-use systems in Amazonia. In Alternatives to Deforestation: Steps to Sustainable Use of the Amazon Rainforest, ed. A. Anderson, pp. 24–42. New York: Columbia University Press.

USDA. Plants Database. http://www.plants.usda.gov/. Accessed on February 2006.

Vázquez-Yanes, C., Batis Muñoz, A. I., Alcocer Silva, M. I., Gual Díaz, M., and Sánchez Dirzo, C. 1999. Árboles y arbustos potencialmente valiosos para la restauración ecológica y la reforestación. Report J084. México: CONABIO – Instituto de Ecología, UNAM.

Vieira, I. C. G., Uhl, C., and Nepstad, D. 1994. The role of the shrub Cordia multispicata Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazônia. Vegetatio 115:91–99.

Villagra, P. E., Marone, L., and Cony, M. A. 2002. Mechanisms affecting the fate of Prosopis flexuosa (Fabaceae, Mimosoideae) seeds during early secondary dispersal in the Monte Desert, Argentina. Austral Ecology 27:416–421.

Villatoro, V. R. A. 1998. El Cuaulote (Guazuma ulmifolia Lam.) como Recurso Natural Antimicrobiano. Licenciatura thesis. Universidad de Ciencias y Artes de Chiapas, Tuxtla Gutiérrez, Mexico.

Wiegand, K., Jeltsch, F., and Ward, D. 1999. Analysis of the population dynamics of Acacia trees in the Negev desert, Israel with a spatially-explicit computer simulation model. Ecological Modelling 117:203–224.

Winrock International. http://www.winrock.org/. Accessed on February 2006.

Wunderle Jr., J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223–235.

Zamora, S., García, J., Bonilla, G., Aguilar, H., Harvey, C. A., and Ibrahim, M. 2001. ¿Cómo utilizar los frutos de guanacaste (Enterolobium cyclocarpum), guácimo (Guazuma ulmifolia), genízaro (Pithecellobium saman) y jícaro (Crescentia alata) en alimentación animal? Agroforestería en las Américas 8:45–49.